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HYBRIDISM IN THE GENUS VIOLA.

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(Plate 58.)

AT the close of my "Notes on New England Violets" in RHODORA, vi. 17, I ventured to suggest that the newly recognized species of blue stemless violets occasionally produced hybrids. Another season of diligent study of this problem, both in the field and in herbaria, has brought to light numerous facts that confirm this theory. Indeed the evidence, when taken in all its detail, seems to place the conclusion beyond any reasonable doubt. The object of the present paper is to report some of these facts and to present the evidence.

There is a widespread reluctance on the part of American botanists to regard an intergrading form as a result of natural hybridism. The systematists of the Old World have far less prejudice, perhaps because they have studied for a longer time and with more care and thoroughness the behavior of their species in the field. The burden of proof is, of course, on the advocates of the supposed hybrid; but that proof should be considered with candor, and not thrust aside from a preconception that hybridism is most improbable. For if hybrids ever occur in a state of nature, and few will deny it altogether, we should expect them to occur among the twelve or fifteen segregates of the old *Viola cucullata-sagittata* group. These segregates are so closely allied, that Dr. Gray, who was acquainted with most of the extreme types, recognized only two polymorphous species with intergradient forms, and that even to-day after prolonged study experts are widely apart as to the delimitation of species. The floral structure indicates that the petaliferous flowers are incapable of self-fertiliza-

tion; and when colonies of two species grow closely intermingled, interbreeding is what might be reasonably anticipated.

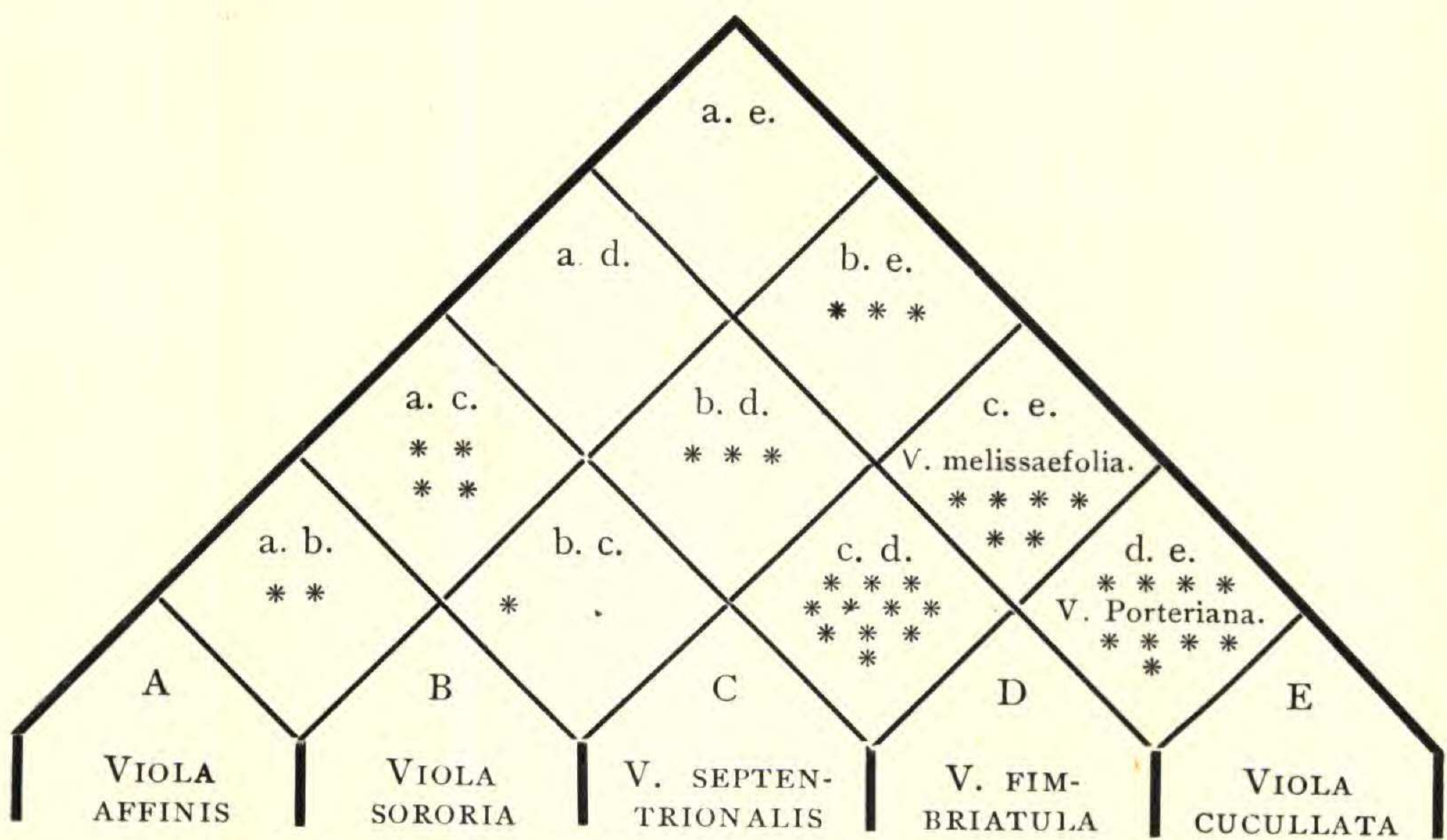
In the present paper I shall restrict the discussion to the behavior of the five species of this group that are most abundant in Western Vermont, and that have naturally been studied in the field with most assiduity. I name them with their contrasting characters in the following table:

	V. AFFINIS ¹	V. SORORIA	V. SEPTENTRIONALIS	V. FIMBRIATA	V. CUCULATA
PLANTS:	glabrous	pubescent			glabrous
LEAVES:	cordate-acuminate	broadly cordate-ovate	ovate-oblong	cordate	
SPURRED PETAL:	with few or no hairs	bearded		beardless	
CLEISTOGAMOUS PEDUNCLES:	horizontal or decumbent		erect or ascending		
CLEISTOGAMOUS FLOWERS:	ovoid-acuminate	sagittate		subulate	
CLEISTOGAMOUS CAPSULES:	oblong usually mottled with purple	subglobose	oblong always green		
CL' ST. SEPALS:	lanceolate	ovate-lanceolate	narrowly lanceolate		
AURICLES:	short, inconspicuous	long, spreading, hispidulous		long, not spreading	

The number of possible combinations in pairs of these five species will be found to be ten. In general, if n represent the number of species, and N the number of possible pairs, we have the formula, $N = \frac{1}{2} n(n - 1)$. That is, among twelve species of *Viola* there would be 66 possible ways of hybridizing. If there were twenty species of *Crataegus* so nearly allied that a cross could be effected between any two of them we might have possibly 190 hybrids.

¹ *V. venustula*, Greene, is found not to be specifically distinct from *V. affinis*, Le Conte, as understood by Prof. Greene, or from *V. obliqua*, as interpreted by Mr. Pollard in the Britton Manual.

This may be represented graphically by writing the five species, as above, in equal spaces, and then drawing from the extremities of these spaces straight lines obliquely upward to the right and to the left. There will thus be formed ten squares, each of which may represent the hybrid that might arise from crossing the two species between the sides of the square produced downward. Thus, in the diagram below, the square marked "a. c." would represent the form obtained by crossing A and C; i. e., *V. affinis* × *septentrionalis*.



Asterisks in the several squares indicate the number of different stations in which the hybrid is believed to have been found; from which it would appear, if my conclusions are sustained, that out of ten possible hybrids eight have actually appeared, and in most cases more often than once. A somewhat detailed account of these eight hybrids, of the associated plants, and of the circumstances attending their discovery is herewith presented.

I. *VIOLA SEPTENTRIONALIS* × *FIMBRIATULA*. A deserted clearing on the mountain side above East Middlebury, partly covered with blackberry bushes and young pines, has been a favorite station for *V. septentrionalis*; and in the more open spaces were to be found also numerous plants of *V. fimbriatula*. Here in the spring of 1902 I noticed in a tract of about four square rods a number of plants that in leaf-outline and in size and color of flowers were quite intermediate between the two species just named. The cleistogamous flowers and

fruit, which were carefully studied the following season, presented the same intermediate characters; being greenish in general color like the one parent, but showing in varying degrees blotches and dots of purple like the other parent. I have again watched the plants, in their wild state and under cultivation, during the past season, and in all their stages of growth they have presented no characters not found in one or the other of the associated species, with one exception — the plants were nearly sterile. The capsules contained on the average only one eighth the normal number of seeds; though along with these seeds could be seen on each of the three valves from ten to fifteen aborted ovules.

Quite similar plants were discovered in August, 1903, in a rocky pasture near the village of Middlebury. The pasture has been in use for over a century; but the thin uneven soil of the ledges has never been plowed, and is more or less overgrown with weeds and shrubs. For a stretch of a hundred rods along this tract are to be seen colonies of *V. septentrionalis* and of *V. fimbriatula* growing intermingled. With them are found twenty or thirty plants that are so distinct from either that by the leaf or the flower they can be told at a distance; and yet on examination they are seen to be exactly intermediate. In the late summer they produce numerous cleistogamous flowers and fruit, but nine-tenths of the ovules remain unfertilized. One of these plants is figured in plate 58, in which may be seen the intermediate character of the leaf, and the dwarfed, almost sterile, condition of the capsule as compared with the parent capsules.

The hybrid has also turned up in two other stations in the vicinity of Middlebury. I have noted also the following dried specimens, which I regard as identical with the Vermont plants: — "Sandy open woods," Orono, Me., July 3, 1897 (*M. L. Fernald*, N. E. Bot. Club Hb.), June 4, 1898, no. 2256, and Sept. 5 & 16, 1898, no. 2706 (Gray Hb.); "Dry open woods," Cape Elizabeth, Me., May 11, 1902 (*M. L. Fernald*, Gray Hb.), in both stations the parent forms also were found; "Dry open hillsides near Gap Mt.," Jaffrey, N. H., June 13, 1898 (*B. L. Robinson*, no. 658, N. E. Club Hb.); "Glade in dry pine woods," Seabrook, N. H., May 29 & July 2, 1899 (*A. A. Eaton*, Nat'l Hb.); near Winchendon, Mass., Sept. 3, 1895 (Nat'l Hb.), *V. fimbriatula* is on the same sheet; "Dry soil, pine woods," Amesbury, Mass., June 24, 1899 (*A. A. Eaton*, Nat'l Hb.), *V. septentrionalis* was collected by him at same time and place.

Last June I received among other plants three specimens of what seemed to be this hybrid from Mr. L. W. Watson of Charlottetown, Prince Edward Island. But the trouble was that though *V. septentrionalis* was common, *V. fimbriatula* had never been reported from that region, and was not known to occur in the Province of Quebec, or in northern Maine and New Brunswick. At my request Mr. Watson kindly revisited the station, and succeeded in finding there excellent specimens of *V. fimbriatula*. We are taught in inductive logic that one of the best possible verifications of an hypothesis is its ability to anticipate the discovery of facts not before observed.

2. VIOLA FIMBRIATULA × CUCULLATA. This I found in Salisbury, Vt., along a trout brook that crossed a sterile pasture at the base of the mountains. Along the edge of the water and in moist hollows *V. cucullata* was common, with short petioles and peduncles when growing in the open, and with long petioles and peduncles when growing in the shade of alders. On the drier knolls back from the brook were colonies of *V. fimbriatula*. Beside them I observed last May plants with wider leaves and larger less decidedly purple flowers marked with a ring of dark-blue at the center. They were examined again in August, and some eight of the plants removed to the garden; the cleistogamous flowers and fruit of autumn, as well as the foliage and the vernal flowers, revealed a plant midway between the two familiar species with which it grew; but no capsule ripened more than four seeds.

I also collected a similar plant in Cheshire, Berkshire Co., Mass., Aug. 26, 1903. *V. cucullata* was found near by, and *V. fimbriatula* is a common plant of the region. The specimen has two green fresh cleistogamous flowers, three somewhat more advanced but brown and withered as though entirely unfertilized, and one green capsule shorter than the sepals and containing only three seeds but numerous aborted ovules.

Just such a plant as these is described and figured by Mr. C. L. Pollard in the Bulletin of the Torrey Club (xxiv. 404) as *Viola Porteriana*. It was collected at Bushkill Falls, Pa., May 31, 1897. Mr. Pollard in the article states that an abundance of *V. fimbriatula* was collected on the same excursion; and I have noted in the National Herbarium and the Bronx Park Herbarium specimens of *V. cucullata*, collected at the same place and time, one by Mr. Pollard and one by Dr. Britton. Profr. Greene (Pitt. iii. 256) undertakes

to identify this with *V. dentata*, Pursh, and Mr. Pollard has accepted this name for his plant in the Britton Manual. Whether there is sufficient warrant for this identification or not, I am confident that the Bushkill plant will prove to be a not infrequent hybrid between *V. cucullata* and *V. fimbriatula*.

I would cite as further instances the following specimens: Dryish hillside in open woods, Cumberland, Me., June 27, 1902, (*E. B. Chamberlain*, N. E. Club Hb.); Jaffrey, N. H., July 25, 1896, (*Walter Deane*, N. E. Club Hb.); Jaffrey, N. H., July 4, 1897, (*B. L. Robinson*, no. 657 Gray Hb.), "Transitional form between *V. fimbriatula* and (?) *V. cucullata*"; Dry woodland, Indian woods, East Lyme, Ct., June 19, 1900, (*C. B. Graves*, 119, Gray Hb. and Hb. E. B.); Granby, Ct., July 10, 1903, (*C. E. Bissell*, no. 8299); Stafford, Ct., Aug. 26, 1903 (*C. E. Bissell*, no. 8269).

3. VIOLA SORORIA × FIMBRIATULA. This plant first attracted my attention in May, 1902, growing at the base of a ledge in a neglected pasture. The foliage and the color of the flowers at once distinguished it from the plants of *V. fimbriatula* with which it was intermingled. At the same time its narrow leaves and prominent stipules separated it from *V. sororia* which grew about twenty feet distant. I took but few specimens, as the colony was not a large one; some of these I sent to Mr. Pollard, querying if it might not be a hybrid. He considered it more probably a new species. I have frequently visited the station since, and find that the fruit shows unmistakable marks of *V. sororia*. The plant much resembles *V. fimbriatula* × *septentrionalis*; but the less ciliate sepals and their smaller appressed auricles serve to distinguish it. It is less sterile than most hybrids, but I have never found a capsule that contained more than half the normal number of seeds.

I place with this specimens collected in Alstead, N. H., July 15, 1899, by Mr. Fernald (no. 335, Gray Hb. & N. E. Club Hb.). I would also call attention to a quite similar plant collected by Mr. Witmer Stone at Media, Pa. (no. 5147) and at Chadd's Ford, Pa., July 5, 1903 (no. 5150), and published by him as *V. fimbriatula aberrans* (Proceed. Acad. Natural Sci. Philad., Oct., 1903, p. 683, Pl. xxxvii, fig. 4-6.) Mr. Stone writes, regarding his 5150, "I think *V. papilionacea* did grow in the vicinity; *V. fimbriatula* was there in abundance; and my surmise was that my plants were hybrids between the two." I refer to this plant here, as *V. sororia* and *V. papilionacea*

are so closely allied that they might without much impropriety be regarded as phases of one species.

4. *VIOLA AFFINIS* × *SEPTENTRIONALIS*.—My first and most important station for this is Knight's Island in northern Lake Champlain, on which I have camped in summer for many years, and whose two hundred acres I have thoroughly explored. I never observed there but two species of blue stemless violets, *V. affinis* and *V. septentrionalis*; but these grow in abundance in moist thickets of arborvitae, under old apple trees and in moist meadow-land. While studying these species critically in August, 1903, I was perplexed to find several specimens that I could not satisfactorily place in either category. The leaves were too acuminate and narrow for *V. septentrionalis*, but not sufficiently so for *V. affinis*; there was a slight pubescence on the petiole and on the margin of the leaf and on the auricles of the sepals, such as *V. affinis* never had, but not enough pubescence for *V. septentrionalis*. What added to my embarrassment was the fact that I was totally unable to find plump, full grown capsules, though there were plenty of small seemingly immature ones. I carefully weeded and mulched the large clump that I had left growing, and waited for further developments. I visited the station last May and frequently during the following July, and became thoroughly satisfied that the plant was a hybrid between the two species so common on the Island.

A further incident is of interest, as showing that the seeds of this hybrid, though few, are fertile and will produce vigorous plants. When I finally on July 24th dug up the clump for herbarium specimens, I found thirty-three seedlings closely clustered about its roots, bearing each only one or two leaves. These seedlings I carried home and planted; they have all lived and flourished. Many of them produced in September cleistogamous capsules; but all of the capsules show the same paucity of seeds as those on the mother plant.

I found several specimens of this hybrid last May in an open grove of sugar maples near Middlebury. The ground was gay with the large violet flowers of *V. septentrionalis*, and in the moister hollows of the ledge there was an almost equal profusion of *V. affinis*. Careful search revealed intermediate forms. One of these transferred to the garden has produced more than fifty capsules, all showing the characteristic infertility of the hybrid.

I have collected a few specimens of the same thing at a third

station, growing with both parents. But I have failed to discover the plant in any of our large herbaria. However, the fact that *V. septentrionalis* is unknown south of New England, and that *V. affinis* is apparently wanting in eastern New England, would seem to account sufficiently for the non-appearance of the hybrid outside of the Champlain Valley.

5. VIOLA SEPTENTRIONALIS × CUCULLATA.— This is another hybrid necessarily restricted to northern regions. I have found single plants at three widely separated stations, always associated with the parent forms. At one of these stations near Silver Lake, Leicester, Vt., I observed in a large assemblage of *V. cucullata* one plant with broad-petaled violet flowers, strikingly distinct from the other flowers. An examination of the leaves showed decided traces of pubescence. I transferred the plant to the garden, where it has since produced apetalous flowers and fruit in abundance. The long somewhat hispidulous sepals display qualities inherited from both parents, but the capsule bears only from one to six seeds. Lest it may be surmised that the moving of these plants has caused this sterility, I would here state that I have the past season transplanted several individuals of each of the five species under discussion when they were in flower and later, that they have afterward fruited in abundance, and that I have never found upon them a capsule that was not plump and crowded with 40–70 seeds. Violets are transplanted with the greatest ease, if set in moist shaded soil, and grow luxuriantly under proper culture.

I received last May from Mr. Watson of Charlottetown, P. E. I., live specimens of *V. melissaefolia*, Greene (Pitt. v. 103) from the type station. As these plants developed in the summer, they turned out to be a good match for the Silver Lake plant that I had also under cultivation. The leaves had the same scanty finely appressed pubescence and ciliation, the petioles the same sparse villose hairs, the capsules the same narrow slightly hispidulous sepals and the same paucity of seeds. The closing sentence of Prof. Greene's note shows that the plant suggested to his mind both of the species here regarded as the parent forms.

I also place here without much hesitation a remarkably robust plant, collected only in petaliferous flower: "Sandy interval, Fort Kent, Me., June 16, 1898" (*M. L. Fernald*, no. 2254, Gray Hb. and N. E. Club Hb.). It has peduncles somewhat longer than the

minutely ciliate and slightly pubescent leaves; the cleistogamous flower is nearly as long and slender as in *V. cucullata*, but with slightly hispidulous auricles, somewhat as in *V. septentrionalis*.

Dr. James Fletcher, the botanist of the Dominion Experimental Farm at Ottawa, who has given much expert study to the violets of Canada, showed me when I visited him last September, a potted plant of this hybrid that came from St. Stephen, New Brunswick. A fine photograph taken last May shows over thirty large flowers on slightly hairy peduncles but little taller than the leaves, and confirms Dr. Fletcher's statement that it is one of the most beautiful of our violets. Mr. Watson and Mr. Fernald have both spoken in similar praise of their respective finds. It is a promising plant that merits the attention of the florist.

6. *V. SORORIA* × *SEPTENTRIONALIS*. I have not as yet succeeded in finding this hybrid in more than one station. This was in a thicket on a narrow terrace of fine silt bordering the river above Middlebury. The plants were growing with a large colony of nearly glabrous *V. sororia*, a form that might pass as *V. papilionacea*. A few rods farther up the stream was to be seen *V. septentrionalis*. The hybrid is distinguished from the plants with which it grew by the narrower leaves, finer pubescence, somewhat spreading auricles of the sepals, and the uniformly stunted and often distorted capsules containing mostly aborted ovules. The plants have not been seen in flower, and require further study.

7. *V. AFFINIS* × *SORORIA*. This has turned up in two stations, fifty miles apart. The first was on a narrow wooded island of four or five acres, in northern Lake Champlain. On the north end of the island is a large lagoon of stagnant water made by the joining of two sand-bars driven northward by wave-action from the two sides of the island. In the moist leaf mould on the borders of this pool are to be seen luxuriant specimens of *V. affinis*, some plants in May bearing each as many as forty petaliferous flowers. A little farther back in drier and more shaded spots are colonies of *V. sororia*; and these are the only two species of blue stemless violets to be seen on the island. Not far from them I discovered, Aug. 6, 1903, a colony of plants intermediate in foliage and pubescence. At the time I did not suspect its relationship with the other forms; I fancied when I noticed its scanty pubescence, that I might have found the long sought for *V. papilionacea*, and destroyed most of the plants in a

vain effort to get good fruit. The capsules all seemed but half-grown; though as it afterward appeared many of them contained ripe seed. Subsequent study of the plants preserved leaves no doubt in my mind that they are the result of a cross between the two associated species.

The other station for this hybrid is in my own dooryard. For many years I had admired a large patch of blue violets growing in moist loam under a large appletree. The plants were cespitose and numerous, and flowered profusely in May, presenting almost a continuous sheet of blue. Until recently they have been to me a great puzzle; I could not satisfactorily place them with any of the common species of the region. I concluded finally "it must be" *V. papilionacea*, an opinion that both Mr. Pollard and Dr. Robinson were disposed to confirm. But the leaves were too small and too pointed, the sepals too attenuate, the capsules too small and purple, when I compared them with specimens of *V. papilionacea* from the Middle States. Further investigation the past season solves the problem. I find (1) several plants that are undoubtedly *V. sororia*, bearing pale-blue flowers, large broad pubescent leaves, large oblong capsules with ovate-lanceolate sepals and abundant seeds; (2) more numerous specimens of genuine *V. affinis*, bearing smaller acuminate perfectly glabrous leaves, violet-blue flowers, small, short oblong capsules with lanceolate sepals and abundant seeds; (3) still more numerous plants, bearing leaves intermediate in outline, size and pubescence, and capsules that are small often one-sided and relatively infertile. The average number of seeds in ten capsules (all that were mature on one plant), was six and two tenths.

8. *V. SORORIA* × *CUCULLATA*. On May 20, 1903, in Cheshire, Mass., (alt. 1200 ft.), I found a large clump of a strange violet, bearing numerous large blue flowers, growing in moist rich soil under a wild appletree along the roadside. The plant was nearly glabrous, the peduncles somewhat longer than the leaves, the sepals lanceolate. I was at a loss whether to call it *V. cucullata* or *V. sororia*; and hoping to remove the perplexity by getting mature fruit, I revisited the station the following August. But in this I was for the time being disappointed; for the capsules, though numerous, were all small, imperfect and few-seeded. The long auricles and erect peduncles pointed to *V. cucullata*, while the pubescence of the petioles, more manifest than in May, pointed to

V. sororia. Apparently my troublesome plant is a cross between these two species, both of which were growing in the immediate vicinity.

The same hybrid was found when in flower last spring in two other stations, associated with the parents. In both cases plants were transferred to the garden, and developed characters during the autumn that are in perfect accord with their supposed origin.

I have gone, somewhat tediously I fear, into these details of personal experience, as I have felt that I could in no other way adequately present the great mass of circumstantial evidence that to my mind establishes the theory of occasional hybridism in this group of plants. And this evidence, as the instances increase in number, has a cumulative force. A single instance of a plant nearly sterile and quite intermediate between two associated species might not bring conviction as to its hybrid origin. But when forty or more such cases are observed, always under similar circumstances, the evidence has a logical force well nigh irresistible.

Along the southern New England coast and farther south are found at least six other species of *Viola* in the same group with the five under discussion. Are these six species equally guilty of hybridism with each other, and with any of the five here discussed with which they may chance to associate? This is a question so grave and so complicated as to require a separate paper for its discussion.

MIDDLEBURY COLLEGE.

EXPLANATION OF PLATE 58.—*Viola fimbriatula* × *septentrionalis*: *a*, autumnal state showing open capsule with seven seeds and numerous aborted ovules. *V. fimbriatula*, J. E. Smith: *b*, leaf; *c*, mature capsule; *d*, same open, showing normal number of seeds. *V. septentrionalis*, Greene: *e*, leaf; *f*, mature capsule; *g*, same open, showing normal number of seeds.

A NEW SPECIES OF BLACKBERRY.

W. H. BLANCHARD.

I WISH to report a new blackberry which I think is sufficiently common and wide-spread, as well as constant in its characteristics, to merit a name and take its place with the five or six best marked North American species. Probably every botanist in New England